

REPRODUCTIVE BIOLOGY OF THE PRICKLY FOREST SKINK, *GNYPETOSCINCUS QUEENSLANDIAE*, AN ENDEMIC SPECIES FROM NORTHERN QUEENSLAND

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Cunningham, M. 1993 12 24: Reproductive biology of the Prickly Forest Skink, *Gnypetoscincus queenslandiae*, an endemic species from northern Queensland. *Memoirs of the Queensland Museum* 34(1):131-138. Brisbane. ISSN 0079-8835.

Examination of morphology, reproductive state and skeletochronological markings in specimens of a rainforest skink, *Gnypetoscincus queenslandiae*, in the Queensland Museum, reveals a sex ratio of 1:1.5 (♂♂:♀♀); that the sexes can not be distinguished by any single morphological trait; females mature at about 55 mm (SVL); and immature females produce many small (<2mm diameter) ovarian follicles. As females approach maturity increasingly large ovarian follicles are produced, but in mature females the number of ovarian follicles produced is independent of size. Clutch size increases with size of mature females. The number of vitellogenic follicles produced is significantly correlated with clutch size. Breeding is seasonal on the Atherton Tableland. A suggested reproductive cycle for this viviparous skink on the Atherton Tableland, is presented. A significant linear regression indicates a high correlation between size and the number of haematoxylinophilic lines in transverse sections of the femur. □ *Gnypetoscincus queenslandiae*, rainforest ecology, reproduction, skeletochronology, Scincidae.

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A well preserved museum specimen, accompanied by accurate records of location and date of capture, provides a snapshot of an animal's physical state at a particular time. A collection of these specimens gives a broader picture of seasonal, size related and geographic variation in a population of these animals. In this way museum collections may provide valuable information on the ecology of cryptic or poorly known species.

One such species is the Prickly Forest Skink, *Gnypetoscincus queenslandiae*. This nocturnal, live bearing lizard is endemic to the rainforests of the Australian Wet Tropics (Cogger, 1992; Nix & Switzer, 1991). Because it is found in or under rotting logs, this species is difficult to study in the field. Greer (1989) describes *G. queenslandiae* as 'one of the most ecologically buffered terrestrial reptiles in Australia' and continues 'given this presumably relatively aseasonal microhabitat, one could ask what has happened to those biological activities that are generally seasonal in less buffered species'.

In several areas of the Wet Tropics, especially the Atherton Tableland, much of the original forest has been cleared for agriculture, grazing and settlement (Winter et al., 1987). *G. queenslandiae* is a common inhabitant of the remaining rainforest, and is thus a suitable species for the study of this habitat fragmentation. The aim of this project was to elicit information on the reproductive biology and demography of *G.*

queenslandiae for later use in ecological and genetic models of the effects of habitat fragmentation. This was done through the examination of a series of this species in the Queensland Museum. Details of these specimens are available from the Queensland Museum database.

METHODS

G. queenslandiae (n=160) from 24 sites in the Wet Tropics were examined. The majority (n=118) were from 18 sites on the Atherton Tableland (17°10'-17°35'S 145°30'-145°45'E), an undulating plateau with an altitude of 700m-900m. Twenty-nine skinks were collected from upland sites to the north (three sites: n=23) and south (one site: n=6) of the Atherton Tableland. A further thirteen were collected from two lowland sites: one at a similar latitude to the Atherton Tableland (Bellenden Ker: n=6) and one site in the northern Wet Tropics (Daintree: n=7). Skinks had been obtained between 1963 and 1992 in February, April, June, September, November and December. Samples collected from the same site at different times were available from only four sites.

The snout-vent length (SVL) of each skink was measured with electronic callipers. Each specimen was then dissected for examination of the reproductive tract. Males were distinguished from females by the absence of oviducts running

forward along the body wall from the gonads, the absence of enlarged ovarian follicles and the presence of a cream coloured epididymis. For each male, only a qualitative assessment of the state (turgid or flaccid) and size (small or enlarged) of the epididymis was recorded. Females were recorded as gravid (possessing oviducal eggs) or not gravid (without oviducal eggs). In addition, the following measurements of reproductive state were recorded for each female: I - Clutch size (the number of oviducal eggs); II number of greatly enlarged (>2 mm diameter) ovarian follicles; III number of enlarged follicles, between 1.5 mm and 2 mm in diameter; IV number of ovarian follicles between 0.5 mm and 1.5 mm in diameter; and V number of small follicles, less than 0.5 mm in diameter.

These classes were determined from the observed size distribution of developing follicles, and correspond to the follicular growth stages described for the Diamond-backed Water Snake, *Natrix rhombifera*, (Betz, 1963) and the latter five classes described for several tropical snakes (Zug, 1979). Oviducal eggs (class I) were a golden yellow colour and always larger than 5 mm; class II follicles were a creamy yellow colour; classes III, IV and V were white. The diameter of each ovarian follicle was determined using a dissecting microscope.

To assess the relationship between size and relative age in *G. queenslandiae*, the left femur from fourteen specimens (representative of the range of sampling locations and size within each sex), was removed for skeletochronological analysis. Each femur was decalcified in formic acid and formalin, and vacuum embedded in wax. Transverse sections were taken from the mid-diaphysis of these bones, mounted on slides and stained for 15 minutes with Delafield's haematoxylin and for 10 seconds with Eosin. These were examined under a compound microscope, to record the number of haematoxylin stained concentric rings in the compact bone of each femur.

ANALYSES

A Chi square test was used to compare the observed sex ratio in the total sample, with an expected 1:1 ratio. Morphological differences between sexes were assessed by Canonical-Discriminant Analysis. This analysis finds the maximum difference between groups (in this case males and females) based on a weighted combination of variable characters, measured on each

individual. Canonical-Discriminant Analysis may demonstrate separation among groups that appear indistinguishable in analyses of single variables, due to overlap between groups in the range of each morphological character. A series of meristic measurements (SVL, head length, head width, length of the left tibia, and length of the left fourth toe) and scale counts (lamellae under the left and right fourth toes, left and right supra-ocular scales, para-vertebral scales, and nuchal scales) gathered on these skinks for another study were submitted to the procedure 'CANDISC' in the SAS statistical analysis package (SAS Institute Inc, 1985). In addition to this multi-variate analysis 'CANDISC' provides analysis of variance (ANOVA) comparisons of groups for each morphological variable (SAS institute inc., 1985). These test the hypothesis that differences between the sexes cannot be distinguished from variation within each sex.

Nix & Switzer (1991) report size variation in populations of *G. queenslandiae* from different locations. The SAS procedure 'GLM' (SAS institute inc., 1985) was used to investigate size (SVL) differences between sampling sites by one-way ANOVA. This analysis included only those locations from which five or more samples had been collected. The mean size of gravid females (with oviducal eggs) was compared with that of all other females from the Atherton Tableland, using Student's t-test, generated by the SAS 'TTEST' procedure (SAS institute inc., 1985). This analysis tests the null hypothesis that gravid females do not differ in size from other females.

Pearson product-moment correlation coefficients, generated by the SAS procedure 'CORR' (SAS institute inc., 1985), were used to compare size of female skinks with number of eggs or ovarian follicles carried by those females, for each class defined above. These analyses test the hypothesis that the number of eggs and ovarian follicles is not correlated with SVL. A Chi square test of homogeneity was used to investigate temporal variation in the proportion of gravid females in the Atherton Tablelands samples, and to test the probability that this variation could be due to random sampling.

Finally, the procedure 'REG' in SAS (SAS institute inc., 1985) was used to generate simple linear regressions of the number of femoral bone rings against size, SVL, for all samples and for those from the Atherton Tableland alone. These regressions are used to predict the expected number of femoral bone rings from a skink of known size.

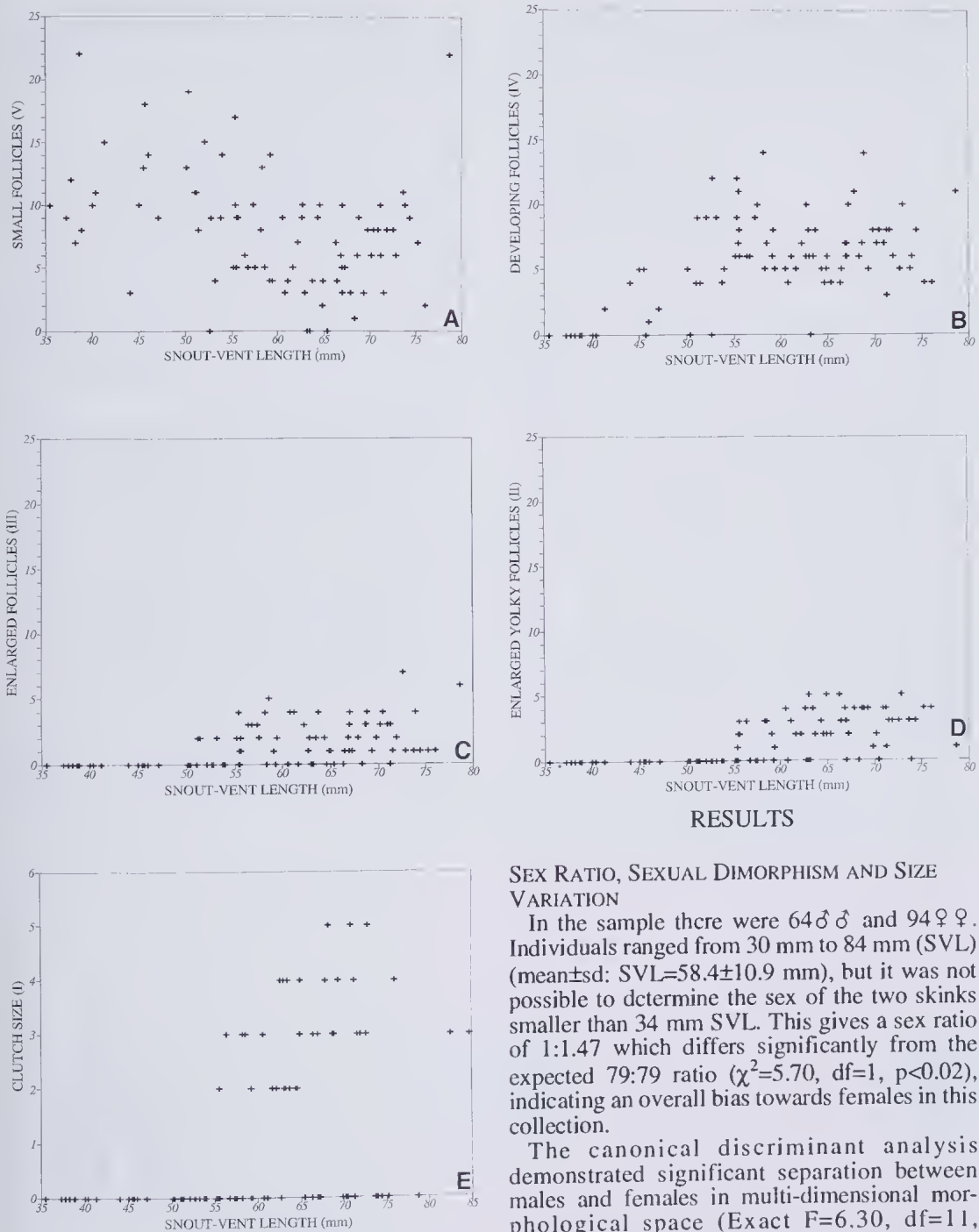


FIG. 1(A-E). Plot of clutch size and number of follicles in each size class against SVL for all females.

RESULTS

SEX RATIO, SEXUAL DIMORPHISM AND SIZE VARIATION

In the sample there were 64♂♂ and 94♀♀. Individuals ranged from 30 mm to 84 mm (SVL) (mean±sd: SVL=58.4±10.9 mm), but it was not possible to determine the sex of the two skins smaller than 34 mm SVL. This gives a sex ratio of 1:1.47 which differs significantly from the expected 79:79 ratio ($\chi^2=5.70$, $df=1$, $p<0.02$), indicating an overall bias towards females in this collection.

The canonical discriminant analysis demonstrated significant separation between males and females in multi-dimensional morphological space (Exact $F=6.30$, $df=11$, $p<0.0001$). This separation was generally not reflected in the univariate tests of sexual dimorphism, with only the number of nuchal scales (NTOT - defined here as the number of scales posterior to, and in contact with, the parietal

Table 1. Correlation between number of oviducal eggs/ovarian follicles and the snout-vent length (SVL) of all females, mature females (SVL > 55 mm) and gravid females (clutch size > 0).

	Sample size (n)	Pearson product-moment correlation co-efficient (r)	Significance probability (p)
ALL FEMALES			
Clutch size(I)	91	0.494	0.0001
Vitellogenic follicles (II)	88	0.622	0.0001
Enlarged follicles(III)	88	0.472	0.0001
Developing follicles (IV)	88	0.508	0.0001
Small follicles (V)	88	-0.349	0.0009
MATURE FEMALES			
Clutch size (I)	61	0.158	NS
Vitellogenic follicles (II)	58	0.257	NS
Enlarged follicles (III)	58	0.130	NS
Developing follicles (IV)	58	-0.042	NS
Small follicles (V)	58	0.124	NS
GRAVID FEMALES			
Clutch size(I)	36	0.390	0.019
Vitellogenic follicles (II)	33	0.299	NS
Enlarged follicles(III)	33	0.115	NS
Developing follicles(IV)	33	-0.021	NS
Small follicles (V)	33	-0.231	NS

scales) showing significant differences between males and females ($F=6.11$, $df=1$, $p=0.015$). Females tend to have fewer nuchal scales (mean \pm sd, ♀♀: NTOT=16.64 \pm 1.83; ♂♂: NTOT=17.43 \pm 1.66). However, the ♀ range (NTOT=13 to 21) is contained in that of ♂♂ (NTOT=11 to 21) and, as this is a discrete character, the expected value of NTOT for both is 17.

Although no significant size differences were detected between the sexes in the above analyses, significant SVL differences were found among sample locations in the ANOVA ($F=4.39$, $df=13$, $p<0.0001$). To further explore these differences the mean of each population was compared with that of each other population using Tukey's studentized range tests calculated by the SAS procedure 'GLM' (SAS institute inc., 1985). The overall type I error rate for these comparisons (the rate at which results are falsely accepted as significant) was restricted to 0.05. Several samples were found to differ significantly in SVL. The skinks from Dowlings' Fragment (17°23'S 145°41'E) are smaller on average ($n=7$:

SVL=43.6 \pm 6.3 mm) than those from other locations, whilst those from Major's Mountain (17°38'S 145°32'E) were generally larger ($n=5$: SVL=72.9 \pm 3.3 mm).

SIZE AND REPRODUCTION

All ♂♂ larger than 50 mm SVL displayed enlarged epididymides (approximately 4.5 mm in diameter), which presumably indicates sexual maturity. None smaller than 45 mm SVL possessed an enlarged epididymis. Among the ♂♂ larger than 50 mm SVL, epididymides were either turgid or flaccid with no clear seasonal or geographic trends. This may indicate a stage in the reproductive cycle, such as the production and storage of sperm, or may be an artefact of collection and fixation.

Of the 71 ♀♀ from the Atherton Tableland, 25 were gravid (mean SVL=66.8 \pm 5.0 mm) and 46 were not (mean SVL=55.5 \pm 11.9 mm). The smallest gravid skink 55.5 mm (SVL); the largest (non-gravid) was 78.7 mm (SVL). Using an estimate of T, modified to account for unequal variance between groups, gravid ♀♀ were found to be significantly larger than others (modified $t=-5.48$, $df=65.9$, $p<0.0001$). No specimen smaller than 55 mm (SVL) had any class I or II ovarian follicles. Class III follicles were found in only three ♀♀ (12%) smaller than 55 mm (SVL), Fig. 1C.

The correlation analysis was performed on three nested groups: all ♀♀, to investigate general size related trends in reproductive state; only ♀♀ >55 mm SVL, to exclude immature skinks ♀♀; and only gravid ♀♀ (clutch size > 0), to compare skinks in a similar physiological

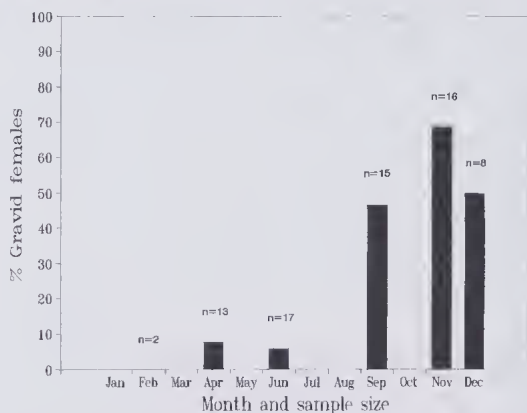


FIG. 2. Temporal variation in percentage of females from the Atherton Tableland carrying oviducal eggs. Sample sizes are given for each month from which collections were available.

condition. Pearson product-moment correlation coefficients for each of these comparisons are presented (Table 1). In the comparisons including all ♀♀, SVL was significantly correlated with clutch size and each class of follicles (Table 1). Clutch size and the numbers of class II, III and IV ovarian follicles increase with SVL, the number of class V follicles decreases with SVL, however, there is considerable variation between similarly sized lizards (Fig. 1A-E). When immature ♀♀ are excluded from the correlation analysis, variation in the number of eggs and follicles appears to be independent of SVL (Table 1). Among gravid ♀♀ clutch size is significantly and positively correlated with SVL (Table 1); large gravid ♀♀ generally carry more eggs than smaller gravid ♀♀ (Fig. 1A). Although the number of vitellogenic follicles (II) was not significantly correlated with SVL in gravid females (Table 1), it was significantly correlated with clutch size ($n=33$, $r=0.536$, $p=0.001$).

FEMALE REPRODUCTIVE CYCLE, ATHERTON TABLELAND

At least 50% of ♀♀ collected from sites on the Atherton Tableland in September, November and December were gravid (Fig. 2). Neither of the two ♀♀ collected in February were gravid. Only one of thirteen ♀♀ collected in April, and one of seventeen ♀♀ collected in June, were gravid (Fig. 2). The Chi square test of homogeneity indicates statistically significant temporal variation in the proportion of gravid females ($\chi^2=22.628$, $p=0.000$).

A temporal trend was also evident in the development of eggs within gravid females. The single gravid specimen collected in June carried small eggs (average egg length 6.0 mm). Several non-gravid ♀♀ collected in June carried very large, class II, follicles (between 4 mm and 6 mm), which were of similar size to small oviducal eggs and were not found in females collected at other times. In gravid ♀♀ collected in September, eggs were larger (average length $=10.7 \pm 1.2$ mm) but showed no obvious signs of fertilisation. Eggs in gravid females collected in November and December were of a similar size to those in September (average egg length 11.8 ± 1.7 mm) and carried developing embryos, up to 5 mm long, surrounded by yolk. The gravid female from April (J31057) was the only individual in the entire sample carrying well developed young, and the only gravid individual to have a clutch size of one. The single foetus found in this female appeared to be fully developed and, although still

encased in the egg membrane, was not surrounded by yolk. This unborn skink had a SVL of 25.9 mm, which was 4 mm smaller than the smallest juvenile skink examined in this study.

This apparent seasonality of reproduction suggests temporal variation in the average size of *G. queenslandiae* on the Atherton Tableland, resulting from an annual pulse of recruitment. The average SVL of *G. queenslandiae* collected from the Atherton Tableland and examined here, shows no such pattern, being highest in April and November, and lowest in September. In some seasonally breeding species the observed sex ratio varies with the reproductive cycle, as gravid females are often more obvious than other individuals (Schwarzkopf & Shinc, 1992; Simbotwe, 1985). In this study the observed proportion of females varies between 50% in February and 73% in December, however, both months have small sample sizes ($n=4$ and $n=11$ respectively). A chi square test of homogeneity shows that there is no evidence for temporal variation in the sex ratio ($\chi^2=1.28$ df=5 $p=0.937$).

BONE HISTOLOGY AND SKELETOCHRONOLOGY

The bone structure of *G. queenslandiae* is similar to that of other squamates (Castilla & Castanet, 1986; Ricqles, 1976; Enlow, 1969). At mid-diaphysis a weakly vascular or non-vascular cortex of periosteal bone surrounds an almost hollow medullary cavity lined with endosteal bone. The periosteal bone consists of a series of peripherally deposited lamellae, among which are regularly arranged, haematoxylinophilic rings or 'rest lines'. Endosteal bone results from the resorption and reworking of the inner cortex and so the amount of endosteal increases with the diameter of the femur. The process of erosion of periosteal bone and substitution with endosteal bone results in the obliteration of some rest lines.

Linear regressions, predicting the number of rest lines from SVL, were statistically significant for both the total sample and for the seven individuals from the Atherton Tableland alone (all samples - $R^2=0.76$, $p=0.0001$; Atherton samples - $R^2=0.77$, $p=0.01$) (Fig 3).

DISCUSSION

The results of this study allow broad estimates of parameters which are vital to the successful application of population models, and which would be difficult to measure under field conditions. These factors include the sex ratio, the clutch size produced, the size at which maturity

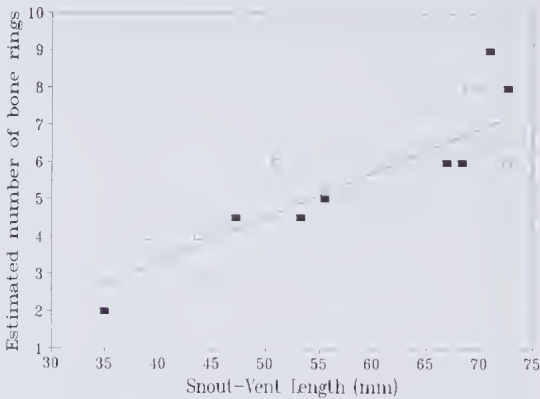


FIG. 3. Plot of estimated number of haematoxylin stained femural bone rings against SVL for individuals from all locations. Open symbols = ♂; closed symbols = ♀. The least squares regression for all individuals (bone rings = $0.12 \pm 0.02 \times \text{SVL} - 1.49 \pm 1.19$) depicted above is significant ($R^2 = 0.76$, $p < 0.001$). The regression including only samples from the Atherton Tableland was also significant (bone rings = $0.09 \pm 0.02 \times \text{SVL} + 0.13 \pm 1.3$, $R^2 = 0.77$, $p < 0.01$).

is attained and the relationship between size and age. These results and others, such as the degree of sexual dimorphism and spatial variation in size, would complement ecological and genetic studies of *G. queenslandiae*.

SEX RATIO

There appears to be a slight bias in the sex ratio towards females. As there is distinct temporal variation in the proportion of gravid females, albeit on small numbers, but no similar variation in the sex ratio, it seems that this observed sex ratio bias can not be attributed to the capture of more gravid females than other individuals. The sex ratio of *G. queenslandiae* would be difficult to determine in the field as there do not appear to be any clear morphological differences between the sexes, although one possible method is the eversion of male hemipenes described by Schwarzkopf (1992).

VARIATION IN SIZE

Significant size differences were found between several populations. Although these may be the result of non-random sampling, it does appear that skinks from the southern Atherton Tableland, particularly from Majors Mountain, are larger than those elsewhere. No significant

size differences were found between latitudinally separated upland populations or between upland and lowland populations, however, the small sample sizes from areas other than the Atherton Tableland may be insufficient to detect such differences. Considerable genetic variation has also been detected between geographically separated populations of *G. queenslandiae* (Moritz et al., 1993). The degree of congruence between this genetic variation and morphological variation could not be examined because of limited sample sizes from matched sites and possible collector bias.

REPRODUCTIVE BIOLOGY

Sexual maturity in females is attained at approximately 55 mm SVL. Males probably mature at a slightly smaller size. Skinks smaller than 50 mm were uncommon in this collection. This may reflect collection bias, rapid growth to maturity, that juvenile skinks are more difficult to locate than mature animals, or a combination of these. In mature females ovarian follicles are always present but vitellogenesis is seasonal. Developing follicles greatly outnumber the number of oviducal eggs, presumably with the remaining vitellogenic follicles being resorbed after the breeding season. According to Shine (1977) the production of more vitellogenic follicles than are ovulated is of adaptive value, allowing an individual to adjust clutch size according to environmental conditions at the time of ovulation. These additional enlarged follicles may also allow multiple clutches

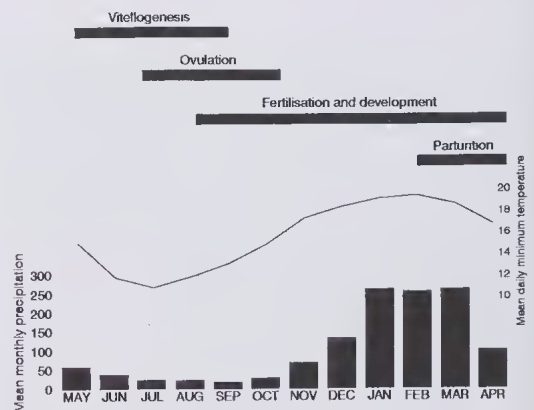


FIG. 4. Reproductive cycle of *G. queenslandiae* on the Atherton Tableland. Vitellogenesis peaks early in the mild, dry season, and is followed by ovulation and fertilisation mid-year. Development of young occurs late in the dry season and throughout the warm wet season, with parturition late in the wet season.

within a breeding season. The latter suggestion is supported by the observed correlation between clutch size (I) and the number of vitellogenic follicles (II).

The correlations between the numbers of ovarian follicles and SVL, when all females are considered, and the lack of any correlations with SVL when only females larger than $SVL=55$ mm are considered, indicates that the number of enlarged follicles (III & IV) produced by immature females increases with size until maturity. The negative correlation between the number of small follicles (V) and SVL, when immature females are included, suggests that the total number of follicles is relatively constant throughout life. As females grow towards maturity some class V follicles become enlarged, and so the number of follicles that remain small decreases.

As in studies of other squamates (Schwarzkopf, 1992; Simbotwe, 1985; Shine, 1977), clutch size in *G. queenslandiae* is correlated with size of females. Life history theory predicts that females should maximise lifetime reproductive output, and that it may be advantageous for a female to use energy reserves for growth rather than breeding, if the probability of survival is high and additional growth will substantially increase future clutch sizes (Schwarzkopf & Shine, 1992). The relationship between clutch size and SVL (Fig. 1A) is consistent with this prediction in that larger females produce either small or large clutch sizes whilst smaller females only produce small clutches. In each of the samples of *G. queenslandiae* considered here a proportion of 'mature' females ($SVL > 55$ mm) were not gravid. In the related seasonally breeding, viviparous skink *Eulamprus tympanum*, Schwarzkopf (1992) found that variability in reproductive output per year was expressed as variation in offspring size, and possibly the proportion of non-breeding females, whilst the average clutch size remained constant across years. The lack of replicate samples from the same sites precluded such an analyses of between-year variation in this study.

SUGGESTED REPRODUCTIVE CYCLE

The skinks considered in this study were collected not only in different months, but also in different years, so it is not possible to distinguish within-year patterns from between-year variation. The predictable climate of the Atherton Tableland and the pattern of temporal variation in the proportion of gravid females and egg development suggest the following seasonal reproductive cycle in *G. queenslandiae* (Fig. 4). Active vitel-

logenesis becomes apparent in June and is followed by ovulation in June and July. Fertilisation and development of foetuses occurs between September and January. Parturition occurs between February and April and is probably accompanied by regression of the vitellogenic follicles that were not ovulated. The time at which mating occurs could not be inferred from the results of this study, as females may store sperm for a considerable time before fertilisation (Fitch, 1982), in this case ovulation.

Reproductive cycles in other tropical skinks are highly variable both between and within species (Fitch, 1982). The primary determinant of seasonality of reproduction in tropical skinks appears to be the seasonality of precipitation (Fitch, 1982). Precipitation on the Atherton Tablelands is distinctly seasonal with average rainfall over 250 mm in January, February and March, and below 50 mm in June, July, August, September and October (measured at Kairi experimental station; AGPS 1988). Temperature is also seasonal on the Atherton Tableland and varies between a mean daily minimum of 10.9°C , with occasional frost, in July, and a mean daily minimum of 19.5°C in February (Kairi experimental station; AGPS 1988). In the reproductive cycle outlined above, embryonic development on the Atherton Tableland would occur during the warm, rainy season, with parturition occurring just before the onset of the mild, dry weather (Fig. 4). In other parts of the Wet Tropics, particularly the Bellen Ker Ra. immediately to the east of the Atherton Tableland, precipitation and temperature are less distinctly seasonal and populations of *G. queenslandiae* from these areas may have different reproductive cycles.

SKELETOCHRONOLOGY

The number of 'rest lines' in the femurs of *G. queenslandiae* shows a clear relationship with size which is roughly approximated by: rest lines = $0.1 \times SVL$ (Fig. 3). Although these rest lines can not be assumed to represent a true index of age as a result of remodelling of the bone, they may be a useful measure of age differences between skinks (Enlow, 1969). Mature individuals had at least five rest lines and no more than nine. If it is assumed that the intervals between rest lines represent constant periods of growth, these results suggest that maturity in *G. queenslandiae* is delayed until quite late in life.

In other species, mainly those from temperate regions, rest lines are formed semi-annually or annually but not less frequently (Castanet et al.,

1988). The observed number of rest lines in *G. queenslandiae* could be used in demographic models as a rough estimate of maximum age, where skinks reach maturity at five years of age and live a maximum of ten years. A sex ratio of 1:1.5 could be used in this model with 75% of mature females breeding each year (maximum number of gravid females with SVL > 55 mm) and each gravid female producing a clutch size of (3.11 = average clutch size). Field studies of size specific mortality and population density would be required to complete this basic model.

ACKNOWLEDGEMENTS

This project was funded by a Queensland Museum Student Research Scholarship. Thanks are extended to Patrick Couper and Jeanette Covacevich for support and access to the museum collections; to Patrick Couper and Craig Moritz for suggestions on possible comparisons and helpful advice on the literature; to Lina Daddow and Zenab Kalel for assistance with the bone histology; and to Damien Broderick, Leo Joseph, Nicole Lee, Craig Moritz, Jeff Miller and an anonymous referee for constructive comments on the manuscript.

LITERATURE CITED

- AUSTRALIAN GOVERNMENT PUBLISHING SERVICE (AGPS). 1988. 'Climatic averages Australia'. (AGPS Press: Canberra).
- BETZ, T. W. 1963 The gross ovarian morphology of the Diamond-backed Water Snake, *Natrix rhombifera*, during the reproductive cycle. *Copeia* 4:692-697
- CASTANET, J., NEWMAN, D. G. & SAINT GIRONS, H. 1988. Skeletochronological data on the growth, age, and population structure of the tuatara, *Sphenodon punctatus*, on Stephens and Lady Alice Islands, New Zealand. *Herpetologica* 44(1): 25-37
- CASTILLA, M. A. & CASTANET, J. 1986. Growth, age and longevity of *Lacerta lepida* assessed by skeletochronology. Pp 331-336. In Roček, Z. (ed), 'Studies in herpetology'. (Charles University: Prague).
- COGGER, H. G. 1992 Reptiles and amphibians of Australia. Pp 498-499 (Reed Books: Sydney)
- GREER, A. E. 1989 The biology and evolution of Australian lizards. Pp 154-155 (Surrey Beatty: Sydney)
- ENLOW, D. H. 1969. The bone of reptiles. Pp 45-80. In Gans, C., Bellairs, A. & Parsons, T. S. (eds), 'Biology of the Reptilia. Volume 1'. (Academic Press: London).
- FITCH, H. S. 1982. Reproductive cycles in tropical reptiles. Occasional papers of the Museum of Natural History 96:1-53. The University of Kansas, Lawrence, Kansas.
- MORITZ, C., JOSEPH, L. & ADAMS, M. 1993 Cryptic diversity in an endemic rainforest skink (*Gnypetoscincus queenslandiae*). *Biodiversity and Conservation*. 2:412-425.
- NIX, H. A. & SWITZER, M. A. 1991 *Tropidophorus queenslandiae*. P.82. In 'Rainforest animals. Atlas of vertebrates endemic to Australia's wet tropics.' (Australian National Parks and Wildlife Service. Canberra).
- RICQLES, A. J. 1976. On bone histology of fossil and living reptiles with comments on its functional and evolutionary significance. Pp 123-151. In Bellairs, A. & Cox, B. (eds), 'Morphology and biology of reptiles. Linnean Society Symposium Series 3'. (Academic Press: London).
- SAS INSTITUTE INC 1985 SAS/STAT user's guide, release 6.03 edition. (SAS Circle: Cary North Carolina)
- SCHWARZKOPF, L. & SHINE, R. 1992. The evolution of reproductive effort in lizards and snakes. *Evolution* 46:62-75.
- SCHWARZKOPF, L. 1992. Annual variation in litter size and offspring size in a viviparous skink. *Herpetologica* 48:390-395.
- SHINE, R. 1977. Reproduction in Australian elapid snakes II. Female reproductive cycles. *Australian Journal of Zoology* 25:655-666.
- SIMBOTWE, M. P. 1985. Sexual dimorphism and reproduction of *Lampropholis guichenoti* (Lacertilia: Scincidae). Pp 11-16. In Grigg, G., Shine, R. & Ehmann, H. (eds), 'Biology of Australasian frogs and reptiles'. (Royal Zoological Society of New South Wales: Sydney).
- WINTER, J.W., BELL, F.C., PAHL, L.I. & ATHERTON, R.G. 1987 Rainforest clearfelling in north-eastern Australia. *Proceedings of the Royal Society of Queensland* 98:41-57
- ZUG, G. R., HEDGES, S. B. & SUNKEL, S. 1979 Variation in reproductive parameters of three neotropical snakes, *Coniophanes fissidens*, *Dipsas catesbyi*, and *Imantodes cenchoa*. *Smithsonian Contributions to Zoology* No. 300.